

COMPARATIVE MORPHOLOGY OF THE BRAIN OF THE SOFT-SHELLED TURTLE (*AMYDA MUTICA*) AND THE ENGLISH SPARROW (*PASSER DOMESTICA*).

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The papers presented before this society have so wide a range that this subject may be admitted with the rest, though its one claim of unity with other papers of the meeting is that the methods and apparatus used are those which it is the primary object of this society to consider and perfect.

The brains studied are too small for thorough observation by gross methods, hence serial sections through the head after decalcification and serial sections stained by the Weigert method have been made, drawn by the camera lucida, and carefully reconstructed into pictures. With these methods all are familiar, as they have been discussed before this society.\*

It may be asked, why should such widely different forms of animal life as a soft-shelled turtle and a sparrow be brought into comparison, the one from the lakes and streams of the middle United States passing a self-controlled, watchful, quiet existence, alternating with rapid and vigorous action, the other, the alert, restless, quarrelsome creature brought from Europe, and become the pest of our door yards.

To the older anatomist, who worked with such remarkable

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\* Material: *Amyda mutica*, gross preparations of the brain of the adult; serial, sagittal sections through the decalcified head (Gage, S. H. '92) of a specimen 6 cm. across the carapace; serial, sagittal, frontal and transverse sections of the head of four specimens 13 cm. across the carapace, stained in hematoxylin and eosin; frontal and transverse sections of the brain of two such specimens, stained by Weigert's hematoxylin method.

*Passer domestica*, adult, gross preparations of the brain and sections in the three planes through the decalcified head; embryos of early and middle stages of development sectioned through the entire head and compared with the entire medisectioned head of specimens of the same age.

The sectioning was done by the collodion method, as modified by Fish ('93) and Gage ('95),

manual skill and accuracy, without the newer appliances, such a comparison would not be surprising, for to him the differences to be seen with the eye alone and the correlation, as far as possible, with the difference in physiological function, were the aims to be sought. Nowhere can a statement showing clearer insight into the great problems now confronting the comparative neurologist be found than that given in the introduction to the great work on the brain by Tiedemann in 1816 ('16). With the rise of Darwinism, and the universal interest in evolution as a process of creation, and with the new methods which (by means of microscopes and microtomes) brought difficult research within the reach of students of average skill, another bent was given to anatomical study. The comparative morphologist has been searching for, and working upon, generalized types, in order to trace the evolution of animal forms from the simple to the complex.

Perhaps now the time is ripe for the pendulum to again swing back, and, with the new thought and the new methods, to make more careful comparisons of widely different forms than before has been possible, in order to obtain from exaggerated structure and highly specialized function, added light upon the problems in which we are all interested.

The work here presented is part of a larger plan in which it is proposed to bring into comparison certain features of the brain of one or more species from each of the great groups of vertebrates, from the period when the brain begins to differentiate from the initial common plan toward the adult condition. This means that many hundreds of successful series must be made and studied. Preliminary work has been done upon certain species of all the great vertebrate groups, and that upon the amphibian brain has been published (Gage, S. P., '93).\* The study of two forms, the turtle and the sparrow, has been carried far enough to permit a preliminary report, leaving details to be filled in as material accumulates.

The problem before us must be attacked in two ways, first, by

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\*As the present paper is a continuation of the work done upon *Diemyx tylos*, *Amia* and lamprey, no further reference will be given to that article.

determining the exact morphological equivalent of each part in the animals compared by means of their development, and by their connections in the adult; second, by close observation of the animals, to determine their normal physiological activities and the correlation of these with the parts of the brain which control them. With the plan in mind a beginning can be made, and below are given some of the points that have been studied.

This work is more or less connected with that done in morphology at Cornell University by Professors Wilder and Gage, and represented in special papers by them and Drs. Fish, Humphrey, Kingsbury and Stroud. The articles which are most closely related to the present are by His, Studnicka, Burckhardt, Herrick, Humphrey and Turner. Herrick ('91) figures the dorsal, ventral and lateral aspect, and six sagittal sections of a young *Aspidonectes spinifer*, another genus of soft-shelled turtles, closely related to *Amyda*. In four pages of text he makes some general comparisons with the brain of other reptiles, and discusses the histology. In general features the brain of *Aspidonectes* agrees with that of *Amyda*, for example, the coalescence of the olfactory lobes. Some points discussed are aside from the main purposes of this paper, others will be further mentioned. Humphrey ('94) shows the external form of the brain of the snapping turtle (*Chelydra serpentina*) both adult and embryo, figures the mesal aspect of this and of the green turtle (*Chelone midas*) with diagrams of fiber tracts. Turner ('91) figures and describes a few points in the anatomy of the brain of a sparrow, as the union of the olfactory lobes, and from the form of the brain in different birds draws conclusions as to their relative rank, placing the sparrow among the more highly specialized. Other articles upon general or special problems touched upon will be referred to in the text.

Among the turtles, the soft-shells are far from the type, not only in external form, but in habits. The body is depressed. The leathery carapace and the combined aerial and aquatic respiration suggest that they may be lonely representatives of a primal stock from which the other turtles are an offshoot, but the union

of the olfactory lobes indicates specialization rather than a primitive condition. As compared with a snapping turtle (Agassiz, '57) it is seen that the small head of the soft-shell does not indicate a relatively small brain, but a more compact arrangement in a cavity which is none too large, while the great jaws and powerful muscles of the adult snapping turtle require a large skull, and leave a spacious cranial cavity in which the comparatively small brain stretches itself out freely upon the floor in such a way as to show all the segments in any view, and thus to make it a brain easy to study (Humphrey, '94).

Among the birds, the group to which the sparrow belongs shows a tendency similar to *Anyda* toward a thinning of the skull, and a crowding and overlapping of the segments of the brain. In the sparrow these are indeed carried to an extreme. Among the more general forms of birds, as the turkey (Turner, '91, Carss, '95) the optic lobes or gemina appear on the dorsal side, but in the sparrow they are visible from the ventral aspect. They are covered by the large cerebrum and cerebellum, which together give an approximately spherical outline to the brain. A comparison of the dorsums of the sparrow and turtle brains (Figs. 19, 28) shows the great difference of form. The turtle's brain shows a portion of all the important parts; the sparrow's brain is so warped from the simple type that the olfactory lobes, the gemina and the oblongata are entirely hidden by the great cerebrum and cerebellum, thus resembling higher mammals. As seen from the meson (Fig. 29), this turtle's brain is one of the most evenly developed and symmetrical brains that it would be possible to find; no part unduly crowds or overtops the rest; each has place each part is equal to the others. In the sparrow (Fig. 20) these conditions are all changed; crowding and disproportionate growth are the rule. In the younger turtle greater crowding of parts exists, and in the embryo sparrow the form more nearly approaches that of the turtle (Figs. 11, 29), while, could we trace still farther back, it would be found that the two brains are quite similar in form, the two in course of development taking different paths, the sparrow's tending to extreme condensation and to ex-

cessive growth of certain parts, the turtle's to uniform growth and comparative elongation.

It is desirable to see what relations of the brain to the body and the habits can be established. The brain of the sparrow has at least twice the size of that of the turtle, while the body weight of the sparrow is only a fraction of that of the turtle. The greater absolute size of the brain is accounted for by the relatively enormous development of cerebrum, cerebellum, geminums and the optic tracts, while the myel and oblongata do not attain to as great size as in the turtle. In the turtle a large part of the activity of the muscles of the body is under the control of the myel and local nerve centers, as can be inferred by the long time that the muscles respond to the stimuli after severing the head, and the long time which it takes to kill the animal by chloroform. In the sparrow death soon occurs by either method. The brain of the turtle is then very largely devoted to the functions which pertain to the head and throat or are under the control of cranial nerves. This turtle can fill its lungs with air and then dive under the water and remain for hours together, the ærial respiration being supplemented by an aquatic (Gage, S. H., '92). In the brain a modified respiratory center corresponding to this habit is to be expected, but this has not yet been actually demonstrated, as too many simpler problems had first to be solved. In the sparrow, in addition to the functions of sensation, etc., there is much more intimate control of the body muscles than with the turtle. The mantle of the brain, the part so greatly developed in man, and forming the highest center for the control of muscular activity, is little developed in both turtle and sparrow. In the sparrow the striatums are the most bulky part of the cerebrum. In them are gathered and from them proceed the fibers, which are comparable to the motor tracts of mammals, which connect the higher with the lower nerve centers. In the turtle, though the striatums occupy a large part of the cerebrum, they and their motor tracts are much smaller than in the sparrow, Figs. 29, 36, 30, 31, 22, 23. From experiments of different kinds it is believed that this part of the brain in mam-

mals has largely to do with the co-ordination of muscular movements. The ceaseless activity of the sparrow, its movements implying rapid and accurate co-ordination certainly point to a large controlling center. The turtle which basks for hours in the sun, or for hours lies at the bottom of the stream, watching for prey or hiding from enemies, only occasionally making a rapid movement and then of a comparatively simple kind, apparently does not need so complex or large a center for muscular co-ordination. The removal of the cerebrums from a frog with subsequent regaining of the power to balance himself and to perform a few acts requiring co-ordinated movements, seems to show that higher centers in the cerebrum are not the only centers, but on the other hand the striatums in the frog are insignificant in size and are simple in structure. Other questions which have arisen as to the relation of function to form can be better treated under special headings.

The differences of form are obvious, but if the problem is viewed in a more fundamental way the tendency is to swing to an extreme and see only the unity of plan in construction and forget the differences. Long ago Wilder\* urged the importance, in brain comparison, of the parts which lie exactly upon the middle plane or meson, and now (Burckhardt '93) this is coming to be accepted as the region in which to seek for those structures which most clearly indicate a common inheritance. Looking closely at the mesal view of these brains (Figs. 20, 29) great landmarks at once appear; the precommissure which unites the cerebrums at the base, the postcommissure at the dividing line between the mesencephal and the diencephal, the crossing of the fourth nerves in the valvula, the cerebellum, the oblongata, the infundibulum and the hypophysis, the chiasma, the epiphysis and the membranous roof of the diencephal. These are different in size

\* The special course on Comparative Neurology given in the spring of 1876 by Professor Wilder, was illustrated by serial sections and by preparations and drawings of the *mesal aspect* of many vertebrate brains made by him during the previous summer and earlier. Since that time his published papers have borne constant evidence of his appreciation of the morphological significance of structures occurring on the meson.

or in location, but from essential relations are found to be homologous structures. A less fundamental similarity consists in the union of the olfactory lobes, while striking differences are found in the condition of the mesencephal, and the presence in the turtle of a very large medicommissure which is entirely lacking in the sparrow.

#### MEMBRANES.

The membranes have been only casually studied. In the adult sparrow they are very thin, crowded together between the brain and the skull. In the embryo sparrow they are not differentiated into distinct layers (see plate I and II), but the spaces between the segments are filled by an arachnoid-like tissue in which are scattered blood vessels. The condition is much like that found in lamprey, *Amia*, etc. The membranes of the turtle's brain are much like those of the snapping turtle (Humphrey, '94); a thick dura, peeling easily from the skull, especially on the dorsum; an arachnoid especially noticeable about the mesencephal; a pia lying close to the surface and in many places, especially over the gemina and cerebellum and between the cerebrums, clearly seen to be attached by filaments (Figs. 32, 34), as occurs in *Diemyctylus*. Blood vessels of considerable size, especially in the sparrow, enter the brain substance and divide into a capillary net work (Fig. 31), as in *Amia* and mammals, instead of forming loops, as in *Diemyctylus*.

#### MEMBRANOUS PARIETES AND PLEXUSES.

The original roof of the brain-tube is a membrane or tela, and in the forms under consideration many remains of this primitive condition persist.

*The metatela (mt.)*, protruding as a sac over the myel in the early embryo sparrow (Figs. I, 7), is a prominent feature, but with development of other parts becomes less so (Figs. II, 17, 18). It would be in this region that a metapore would be looked for, but although the membrane is extremely thin it seems to be continuous, and up to the present no distinct metapore has been

found. In the turtle this sac is present, though not as large as in the snapping turtle (Humphrey, '94). It has a considerable lateral extent and at the sides the cells become attenuated, but in all specimens examined this part was so obscured by a plug of material containing granules that it is impossible to state whether a metapore exists or not.

In the embryo sparrow, between this sac and the cerebellum are a few folds in the membrane, the simple beginning of the *metaplexus* (*mtp.*, Fig. 1). In the older embryos (Figs. 11, 17), this plexus is seen to be greatly developed, and to arise in part of its extent between solid walls, both of which belong to the cerebellum, thus forming a true *epiplexus*. In the adult (Fig. 20), with the growth of the cerebellum it becomes an insignificant feature, both on the meson and as it continues along the caudal border of the cerebellum to the flocculus. In the turtle (Fig. 29), the metaplexus occupies an extensive portion of the metacœle. In its caudal part it crosses the meson as a deep in-folded membrane (Fig. 30), but cephalad it is formed by intrusions of pia and covering endyma through the slit *u* (Fig. 36). The elongated folds interlace across the meson. In the green turtle (Humphrey, '94) the plexus is a nearly drum-head-like membrane with a few slight folds occupying a V-shaped opening between the short cerebellum and the oblongata. A growth caudad of the cerebellum narrowing the V-shape to a slit would produce the result here attained, pushing the lateral part of the plexus into the cavity and crumpling the mesal union into a compact mass at the caudal extremity.

In an early embryo sparrow the roof of the epicœle is a narrow membrane or *epitela* (Figs. 1, 6), which is replaced later by a median lophius, while a raphé-like appearance exists between the two halves. In the turtle such a lophius is a marked feature of the cerebellum and will be discussed under *sulci*.

The membranous roof of the mesencephal, *mesotela* (*mst.*), is found in all stages of the sparrow's growth, becoming exaggerated with age (Figs. 3, 23), while in the turtle it is obscured completely. (See below under *mesencephal*).



The roof of the diacœle always remains membranous. Its original condition, an unfolded tela, is seen in the young embryo sparrow (*dt.*, Figs. 1, 2). The folding which occurs later is in the form of a mesal plate with secondary foldings (*dp.* Figs. 15, 16), a condition remaining unchanged in the adult (Fig. 20). In the turtle the exaggerated tubular condition of the roof of the diencephal described by Humphrey in the snapping and green turtles, and which was originally mistaken for an epiphysis, does not occur. But on the other hand, though ventrad of the epiphysis the plexus takes a mesal position (Fig. 42), most of the plexiform folds are from the lateral walls and are so continuous with the auliplexus as to make a boundary line between the two impossible. The condition in the turtle seems to be one which could be transformed more readily into the mammalian type (Wilder, '89), with two parallel plexuses from the roof of the diencephal, than the condition found either in the sparrow or in *Amphibia* (*Diemyctylus* and *Desmognothus*, Fish, '95) where there is a single mesal plexus.

The roof of the prosocœle involves questions of morphology which will be reserved for the latter part of this paper. There is in both the sparrow and the turtle, a mesal portion of the plexus which will here be called *auliplexus* (Figs. 39, 14, 15), though sometimes called the velum. It gives off the paraplexus on either side. The *paraplexus* in the turtle, outlined faintly in Figs. 29, 36, is of somewhat remarkable form. At the porta it divides into two portions, a dorsal and a ventral; the ventral passes obliquely cephalo-ventrad, to the angle *pc'* in the paracœle, the dorsal sends a branch cephalad even into the rhinocœle, and another branch caudad along the dorso-caudal angle of the paracœle, *pc'''*, to near the tip of the medicornu, *pc.*, Figs. 40-42, 29-31.\* This last-named part has no connection with the *paratela*. In the sparrow the paraplexus consists of a single portion outlined faintly in Figs. 1, 11, 20.

\*In the article by Herrick ('90) on the alligator's brain, no plexus was shown, but it really exists in the young, at least, and is very similar to that of *Amyda*.

In the youngest specimen here figured it is merely a slightly corrugated membrane lying close against the great mesal mass of undifferentiated membrane (Fig. 2). It is noticeable in the older embryo that the union of the auliplexus with the paraplexuses lies dorsad of the porta (Fig. 14).

The *paratela* in both forms is a membrane extending from the porta to near the tip of the medicornu. In the turtle it forms a large thin membrane (Figs. 31, 40-42, *rm.*) of endyma and pia stretched over the thalamus, and could we imagine the object large enough the glistening white of the underlying optic tracts would shine through it. It is bounded dorsad by the fimbria, ventrad by a similar edge or ripa, the tenia, lying next the striatum. (See *sulci* below.) In the adult sparrow it is doubtful if the extensive thin portion of the cerebral wall occupying a similar position can all be called paratela, because it is traversed by bands of fibers which converge toward the base of the cerebrum (Fig. 11), but in the half-grown embryo there is a definite paratela (Figs. 14-16, *rm.*). In the earlier embryo (Figs. 2, 3) the part so designated has a barely appreciable amount of wall which has the general appearance of nervous substance.

#### MEMBRANOUS OUTGROWTHS.

Small pockets, or offshoots of the endymal lining of the cavities, have been observed in both forms, and cannot be omitted, because of the significance which must attach to any structure which exists in these parts, where there is preserved most accurately the original pattern. The embryo sparrow has such a pocket (Fig. 1, R) extending around the dorsal thickened portion of the terma, in which later appears the precommissure. It seems like the *Lobus olfactorius impar* of Kupffer, but no trace of it is found in the later stages. The adult turtle has two pockets, nearly meeting about the common projection, formed by the precommissure and the callosum (Fig. 29). The ventral one is quite deep (Fig. 35, *b*), and is homologous with the preoptic recess of Amphibia. A pocket of endyma caudad of the post-commissure in the embryo sparrow (Fig. 11, S), is a strong

reminder of the pocket of endyma, which in the lamprey extends cephalad of the postcommissure, and in the frog (Ecker '89) and shark occupies a similar position. Their homology has not yet been determined.

The *epiphysis* of the turtle curves cephalad from the roof of the diencephal. Between the postcommissure and supracommissure its occluded tube can be traced to join the endyma of the cavities (Fig. 29). The condition is not as described by Herrick ('91) in *Aspidonectes*, a tube opening "into the canal connecting the optic ventricles with the dorsal part of the third ventricle." It seems as though this must be a misinterpretation, which would not have occurred if transections as well as sagittal sections had been studied. The epiphysis of the sparrow has an elongated stalk continuing to the skull, along with the great growth of the cerebrum (Fig. 20). In the embryo it is nearly sessile, and the tube is open (Fig. 11). The end of the epiphysis in the earlier embryo (Fig. 1) has not yet formed the complex foldings found in the adult. It does not appear from the late formation and slight development of the supracommissure in the sparrow that this is an essential landmark of the entrance of the epiphysis, while in the adult the long stretch of membrane between this entrance and the postcommissure (Figs. 20, 25) shows that variability in the details of arrangement in this region may be expected. In neither of the forms is there any appearance of an eye-like structure in the epiphysis.

It is now known that a *paraphysis* exists in a number of vertebrate groups including the human fœtus (Francotte, '88, '94). It is found in the adult *Amphibia* and the snapping turtle. It also exists in this soft-shelled turtle (Figs. 29, 40). As with the snapping turtle (Humphrey, '94) the character of the endyma lining the epiphysis is different in appearance from that covering the plexuses. It was by this difference alone that it could be distinguished in many sections from the plexuses, a difference very marked in Weigert preparations where the nuclei of the paraphysis stain very deeply. Its function is unknown, but it furnishes another landmark by which may be determined more

exact homologies of parts. In the adult sparrow no trace of this structure was found, but in the younger embryo (Fig. 2) its presence as a minute pocket was clearly seen. The paraphysis in *Anyda*, as in *Amphibia*, lies between the auliplexus with its branches and the diaplexus, but its ramifications, extending both cephalad and caudad make it difficult to state with any such definiteness as with the *Amphibia* the relation of the opening to the cavities. In the young sparrow (Fig. 2) the paraphysis occurs in the midst of a mass which gives off the paraplexuses, and it opens directly dorsad of the portas, *i. e.*, into the aula.

#### RHINENCEPHAL.

This term is used here for convenience alone, since evidence of segmental value is in these forms purely negative. The olfactory lobes of these two forms have a feature in common, that is, they are united across the meson. In the sparrow the union is very close, the cinerea forming a core containing no cavity and showing no indication of division into two halves (Figs. 20, 21, 27), while in the turtle the concentric layers about the cavity of each side are complete, not fusing across the meson (Figs. 30, 31, 37). In the turtle myelinic fibers lie parallel to the meson, but do not cross from one lobe to the other. The lobes are, however, united by a close meshwork, in which a few blood vessels indicate that the condition is secondary. A few cells lie exactly upon the meson, but from the appearance in Golgi preparations they seem to belong to the neuroglia. The glomerular layer of each lobe is separated from that of the other by pia. In the sparrow this union was not found to exist in the younger embryo (Fig. 1), but was fully established in the older (Fig. 11). Thus it appears that this peculiarity of the soft-shelled turtle (Herrick, '91), the higher birds (Turner, '91), and the frog (Ecker, '89), is not one that indicates relationship, but is a condition incident to other specializations, established comparatively late in embryonic development. Without doubt it indicates the less relative importance of olfaction to these highly specialized representatives of different vertebrate groups. The process of degeneration has been carried in the sparrow to an extreme, and

its olfactory lobes, from their intimate union and small size, indicate very little functional activity. In the turtle there are two olfactory nerve roots on each side, a large one from the ends of the lobe, and a smaller one from the caudo-mesal angle (Figs. 36, 37). Each root has its independent glomerular layer, as described by Herrick ('91). The two roots soon unite, and the course of the olfactory nerves so formed continues independently to their distribution in the nose. In the sparrow there is one nerve on each side, and that a small one. The cavity of the cerebrum does not reach the olfactory lobe in the adult sparrow. In the turtle the rhinocœle is large, with a lateral extension (Fig. 31), and it is distinctly marked off from the paracœle by both dorsal and ventral constrictions, while externally the lobes are demarcated from the cerebrum by a slight furrow laterad (Fig. 28) and a deeper one mesad, in which are blood vessels (Figs. 29, 30).

#### PROSENCEPHAL.

In any section of the cerebrum of either form under discussion, it is seen that the mesal and caudal walls are thin. In the adult sparrow, in many parts, they approximate membranes. In either case the greater part of the mass is in the body called here the striatum, in accordance with older usage, though some recent writers (Herrick, '91), propose to call it the axial lobe. Spitzka, ('81) pointed out that in birds the striatum in its growth crowded against the adjacent parts and fused with them. The appearance in the soft-shelled turtle and in a young alligator, and a comparison of sections of the different stages of development of the sparrow, leads to a similar conclusion. While, therefore, the main part of the mass is homologous with the striatum of mammals, the comparatively thin lateral portion fused with it should be excluded. Curving around the endymal surface of the striatum in the turtle, and forming the larger part of the protrusion into the cavities (Plate IV, V), is a portion which seems comparable with the caudatum of mammals, but in the caudatum of the turtle the cephalic end is narrow and the caudal wide, thus reversing

the conditions in mammals (Figs. 38-42); and its caudal tip projects freely into the cavity. In the embryo sparrow a similar elevation can be seen (Figs. 1-4, 11). In the older embryo (Fig. 16), the rest of the striatum has grown so much that the caudatum is less clearly seen, and in the adult it is very slightly raised above the general level.

Following the transections of the turtle's right cerebrum from the caudal tip it is seen that the wall has the form of a Greek delta.



The ventral limb represents the striatum, the right limb the pallium, the left represents the combined hippocampal and tenial borders. The ventral limb is soon increased by the addition of the caudatum (*st.* Fig. 42), which in a few sections more is fused with a part of the pallium (Fig. 41), and can be traced to the olfactory region, where it is gradually thrust away from the endymal surface by the proper olfactory structures. The pallial limb of the delta occupies at first the lateral portion (Fig. 42), but cephalad a free portion is confined to the dorsal aspect (Fig. 38), and is gradually lost in the olfactory region. The mesal limb soon divides into a dorsal, the hippocampal and a ventral, a scarcely appreciable ripa, the tenia, seen at the edge of the striatum (Fig. 42). As the porta is approached, the tenia joins with the wall of the thalamus (Fig. 40) and an outgrowth from this united portion (Fig. 39), apparently a thickened portion of the original terma, hence called termatic, joins with the hippocampal limb (Fig. 38) to form a single mesal limb, thus re-establishing cephalad of the porta, the delta-form. This mesal limb is also lost in the olfactory region. In the *Diemyctylus*, sections show this delta-form of the cavity still more clearly, for the striatal limb is not obscured by the growth of a caudatum. The portion of the mesal wall in *Diemyctylus* was called the callosal eminence, but

here is called the hippocamp. The small hippocampal region of the sparrow is, as in mammals, related to the reduced olfactory lobes, and this segment and the pallial are not well separated in the adult, although in the embryo (Fig. 2) they are distinguishable.

In the mesal views a projection of the outline of the cavity is indicated by interrupted lines. In Fig. 29 an attempt is made to indicate the two wings of the paracele of the turtle which are due to the position of the striatum (Fig. 42). The lateral wing extends quite far cephalad (Fig. 40  $pc'''$ ) while the mesal wing ( $pc$ ) in the neighborhood of the fimbria and paratela can be strictly compared with the medicornu of mammals. The caudo-dorsal angle ( $pc''$ ) demarcating the pallium from the hippocampal region (Figs. 30, 41-42) becomes rounded cephalad (Fig. 38), and caudad it continues to the tip of the paracele. I will refrain from using the term post-cornu for this part because it suggests a close homology with the primate brain, implying the presence of a calcar (Wilder, '89). However, the calcar is due to a total fold of the wall of the cerebrum which does not occur outside of the primates, but the angle which the calcar projects into, and which forms one essential part of the post-cornu, probably existed prior to the intrusion of the calcar. The precornu ( $pc'$ ) dips ventrad so that the cephalic continuation of the cavity into the rhinoccele ( $rc$ ) is from the dorsal portion of the narrowed cavity. In the sparrow a true rhinoccele does not exist in the stages examined, but the projection of the cavity toward the olfactory region is dorsad of a portion of the cavity (Figs. 1, 11, 20,  $pc'$ ) which is homologized with the precornu of the turtle. The medicornu and the lateral wing around the striatum are clear in the embryo sparrow (Fig. 2,  $pc$ ), and the latter becomes much exaggerated in the adult, but in no stage is the caudo-dorsal angle so evident as in the turtle.

#### DIENCEPHAL.

In the turtle the most marked feature of the diencephal is the great mesal union of the two sides by means of the medicommis-

sure. Such a connection is present in mammals and reptiles, but in both it is due to a secondary thickening of parts and arises late in embryonic development, or in man it is sometimes absent. (Wilder, '89). In birds it is not present and hence an unobscured picture of the more fundamental conditions may be looked for in them (see sulci). In the turtle a few very delicate myelinic fibers cross the meson in this commissure (Figs. 42, 36), a condition said to be present in man (Quain, '92). The other commissures, nidi and tracts, which make up the main body of the thalamus, will be discussed later.

The part of the *terma* between the chiasma and precommissure is a thin narrow membrane (Figs. 1, 5, 11, 13, 20, 29). It is much elongated in the sparrow, while the corresponding part in *Diemyctylus* and lamprey is shorter, in *Amia* it is very much reduced. In the last three it forms a part of the ventral wall. At the ventral end of the *terma* occur the optic recesses which, in both sparrow and turtle, form pouches with thin cephalic walls hanging at either side of the chiasma. At the dorsal end of the *terma* in the turtle occurs the preoptic recess (Figs. 29, 35 *b*). This was not found in the sparrow.

In fishes the *infundibulum* reaches its maximum development. It was found in *Amia* that there are from this region two unpaired caudal extensions; a ventral, the *saccus vasculosus*, a dorsal, called by Herrick ('93) the "mammillary body;" and dorsal of them a pair of projections, the *hypoaria*; and a pair extending cephalad and surrounded by the hypophysis. A sulcus continues from these last to the *saccus*. The *Amyda* has from the caudal part of the *infundibulum* three mesal projections (Figs. 29, 36, 42). The ventral has a peculiar wall composed of clear, columnar cells. It is somewhat ramified, and as it is surrounded by the hypophysis it is not strictly comparable with the *saccus* of *Amia* except in position. The hypophysis\* is separated from the *infundibulum* by pia and is composed of two portions, an ectal

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\*The term hypophysis, as here used, agrees with the usage in innumeralia. In mammalia, a part of the brain wall is frequently included in the term or the two parts are distinguished as pre- and post-hypophysis.



and an ental of somewhat different microscopic appearance. The next dorsal of the two mesal pits mentioned is much the wider of the two. Continuing cephalad from the ventral of the three is a sulcus on either side which extends to a point ventrad of the infracommissure, *i. e.*, to a point quite similar in position to the cephalic pair found in *Amia*. In the bird the infundibulum is comparatively much simpler. In the younger embryo (Fig. 1) the hypophysis is composed of tubules, and a duct connects it with the enteron. It lies cephalad of the ventral prolongation of the infundibulum. In the adult (Fig. 20) it is applied along a greater extent of the infundibulum, and the latter has a caudal and a slight cephalic projection. No others were discovered, unless the wavy outline of the caudal boundary of the infundibulum (Fig. 1) indicates such in the embryo. In both animals the infundibulum is far from the fish-like form and particular parts could only be homologized after more thorough study.

#### MESENCEPHAL.

In the turtle the roof of the mesencephal is a solid structure with great commissural systems uniting the gemina (Fig. 29, *gm. cm.*). In the adult sparrow, at the part which lies next the postcommissure there is a slight union of the two gemina across the meson by fibers (Fig. 20 *gm. cm.*), and all the rest of the roof is a membrane which is stretched (Fig. 23) between the widely separated gemina. In the embryo the solid parts of the roof are close together (Figs 1-5, 11) the membrane being a mere narrow strip. The adult condition is a strong reminder of that in the young lamprey, where it was found that not only was the roof a membrane, but it forms a plexus. In the mouse a similar thin membrane was found in this situation by Professor H. E. Summers (Unpublished work done at Cornell University, 1886-8). In the turtle as in the *Diemyctylus*, a trace of this membranous condition can be found in the adult in a small mesal lophius and in cells which extend along the meson far toward the pial surface. Here a curious problem arises. The sparrow, like other higher birds, seems to be pre-eminently a

seeing creature, and the parts connected with vision are all large and well developed except this. In the turtle in which, from general development of parts, vision apparently is far less important, a union occurs along the whole meson, in which great commissural tracts cross from side to side, and mingle with fibers from the optic nerves. Mere stretching or crowding by other parts cannot account for the difference. More fibers could have taken as long a course as between these divaricated gemina had there been continued in the birds the need of so intimate connection of the parts as existed in their reptilian relatives. The significance of this condition, its connection with vision, the question as to whether it arises from atrophy producing reversion to an original type, or whether it is a direct inheritance from a form in which such union never took place, all remain to be studied. In the early embryo sparrow the gemina are prominent upon the dorsal surface (Fig. 1) and have a position and relative size comparable with the adult turtle. In the next embryo (Fig. 11) the relative shape and position have become markedly changed. The cerebrum and cerebellum are not large enough to produce any such crowding as to account for this change, hence the conclusion is reached that it is the inherent growth and development of the gemina themselves that has led to the displacement from their typical position. Compared with the cellular portion of the brain the myelinic fiber tracts are fixed. The optic tracts in the second embryo are well developed with two strands on either side (Fig. 12), one arising near the everted tip of the geminum and crossing entad of the other tract. This ental tract is, in the younger embryo, little developed, and as it has already been seen, the tip of the geminum is also little developed. With a large development in the region of the tip, and with fiber tracts early becoming myelinic, the tendency must be, with the growth of other parts, to hold the tips in a relatively fixed position, thus stretching the thin membranous roof, and leaving the gemina at the level of the base of the brain. The cerebrum and cerebellum in their growth cover the gemina, but do not push them aside. In the turtle two similar optic tracts (see description of Fig. 36) are

found, but neither the ental tract nor the tip of the geminum takes on such marked development. It is observable that the gemina in the second embryo sparrow are really nearly as great in length as in the adult (see description of Fig. 20), that is, before the cerebrum and cerebellum have made much progress toward developing the geminum has approached its maximum size, and this may be adduced as another argument against the theory of crowding.

In the younger embryo (Figs. 2-4) the wall of the geminum is comparatively thin, and the opening from the mesocœle into its lateral recess is large (Fig. 1), in the second embryo the walls are rapidly thickening (Fig. 13) and the entrance into the lateral recess is diminishing (Fig. 11). These processes continue until, in the adult, the recess is constricted and the opening a mere point. One feature of the wall is remarkable. On the mesal surface of the geminum (Fig. 1) is seen a furrow (G); corresponding to this on the endymal surface is a ridge (Fig. 4), which as it passes ventrad becomes wider and divides the recess into two parts (Fig. 5). In the second embryo in the corresponding region of the geminum (Fig. 13, N), there is only one pocket; the other has become consolidated and is represented by a cell-mass. From a comparison of the position of this cell-mass and of the connections of a fiber tract in this region it seems probable that the nidus (q, Fig. 36) of the turtle corresponds to this cell-mass; also that there may be represented the post-geminum of higher forms, and that in all forms at some time a pocket of endyma may close and give origin to the cell-mass of the post-geminum.

In one specimen over an extensive area lying between the letters *q.* and *m. p.* (Fig. 29) the endyma of the two sides has coalesced and degenerated, leaving a narrow tube ventrad, and a somewhat wider one dorsad of it to connect the cephalic and the caudal parts of the brain cavity. It seems like an incipient narrowing to produce an iter like that of the mammalian brain or the narrow mesocœle of the adult sparrow. A pit at the cephalic tip of the oblongata has been identified in the turtle and in embryo

sparrows as the mesencephalic pit (Figs. 1, 11, 29, *m. p.*), but it could not be found in the adult sparrow.

The direct short course taken by the optic tracts in the sparrow has already been mentioned. They retain in the chiasma their relative position (Fig. 12), and in addition there is a distinct tract arising in the thalamus and crossing in the chiasma dorsad of the others. The long course of these tracts in the turtle is as described under Fig. 36. The optic nerves of the turtle are pressed closely together for some little distance, when they turn abruptly toward the eyes. Each is deeply folded upon itself, the pia dipping into the fold. The chiasma and optic nerve of the sparrow are extremely large.

#### OBLONGATA.

For the purposes of this article the limits of the ventral portion of the metencephalic and epencephalic segments will not be considered since no new light has been thrown upon the subject; hence the whole floor of the caudal part of the brain will be considered under the heading *oblongata*, and only a few facts noted with regard to the cranial nerves will be mentioned.

In the turtle all the nerves controlling the muscles of the eye, the third, fourth and sixth, are relatively large, and it is interesting to note that, while every other part of the body, except the swelling throat, may be kept in a condition of apparently absolute quiet, the eye is tirelessly turning as indicated by the horizontal bar across it, with every slight movement of the observer. This turtle seems to have adopted the motto of "eternal vigilance" in place of an armored defence. In the sparrow the third nerve is very large, but the fourth and sixth are relatively small.

In the turtle, as in the mouse, a very large branch of the fifth nerve passes to the tip of the snout. The vibrissæ of the mouse and the long, pointed, comparatively thin skinned tip of the turtle's snout evidently have comparable functions. A large and valuable part of the information carried to the brain must be through this channel. Much of the time the turtle is completely submerged in the water, except the tip of the nose, or if buried

in the sand, the tip of the nose, through which it breathes, is just exposed. In other turtles and in the birds the horny beak cannot be as delicate an organ of touch, and in the sparrow the corresponding branch of the fifth nerve is only of moderate size. In the turtle the fifth nerve has a large Gasserian ganglion. In the sparrow this ganglion is not so large. In the turtle the fifth nerve arises upon the cephalic side of an enlargement of the brain cavity in that position, the seventh and eighth upon the caudal side of the same enlargement, while the tenth is at the widest point of the next succeeding enlargement of the cavity. In the young embryo sparrow similar relations were observed, but in the adult the thickening of the oblongata obscured the appearance. The ninth nerve in the turtle has a ganglion independent of the ganglion of the tenth, while the numerous nerve roots of the ninth unite and then pass into the ganglion of the tenth. The seventh and eighth nerves have much less intimate connection than in the sparrow or in the snapping turtle (Humphrey, '94). The seventh has three branches, the first dividing into two, each of which has an independent ganglion, as does the second branch; the third branch joins the ganglion of the eighth. These ganglia indicate sensory functions, and two of the above-named branches pass into the cephalic parts of the ear capsule, and may really be part of the eighth. In the sparrow the seventh and eighth unite more completely in a ganglion common to both, and the eighth has a very large band of conspicuous fibers, which pass mesad and immediately ventrad of the endyma cross the meson. This is one of the two instances where a commissural or decussational connection across the meson is noticeably greater than in the turtle. The sense of hearing certainly is keener in the sparrow than in the turtle. The turtle will move when a distinct jar is given the vessel containing it, but even quite a loud noise does not appear to give it any uneasiness, while the sparrow is startled by any slight sound.

#### CEREBELLUM.

The function of the cerebellum is still a matter of great doubt, but in the two forms considered the great peduncular tract (32),

(Figs. 11, 13, 36, 30), coming from the alba of the cerebellum and decussating across the meson bends over among the fibers of the eighth, becomes diffuse at this point in such a way as to lead to the inference that certain functions of the ear must in these forms be largely regulated by the cerebellum. The intimate connection of the acoustic eminence and the cerebellum in the *Sauropsida* was noticed by Spitzka ('81). The large, complex cerebellum of the bird and the simple one of the turtle would appear to harmonize with the facts concerning the eighth nerve and the sense of hearing already mentioned, and perhaps also points to a connection with the still only partially understood sense located in the semi-circular canals of the ear.

In the development of the cerebellum of the bird the roof is at first a mere membrane (Fig. 1), the thickened portions not having passed across the meson, a condition which corroborates the position taken by Stroud ('95) and Schaper ('94), that the cerebellum is originally a paired lateral outgrowth. In the next stage the union has taken place across the meson (Fig. 11), and with the exception of a few folia upon the surface, it has a marked resemblance to the turtle's cerebellum, and an even more marked resemblance to that of the alligator, for in that the caudal part bends over more than is the case in the turtle. In the second embryo of the sparrow the pit in the skull (Figs. 13, 17-18) which later will be occupied by the *flocculus* is filled by arachnoid tissue, and the *flocculus* is a mere projection pointing toward the pit, *i. e.*, the bony wall undergoes the modification necessary for the reception of the *flocculus* before that comes in contact with it. In the adult sparrow the cavity of the cerebellum is small and at the middle is actually closed by the crowding of parts together, the endyma having become obliterated (Fig. 20). There are thirteen folia seen at the meson. Traced laterad in serial sagittal sections it is seen that the central folia, the seventh and eighth pass slightly beyond their neighbors giving the appearance of a lateral lobe, while the caudal ones, the eleventh to the thirteenth, forming the caudal rim of the cerebellum, fuse laterad and at the tip of the lateral recess of the cavity form the

*flocculus* by uniting with the lateral extension of the cephalic part of the cerebellum. The *flocculus* was originally given the name because of its resemblance to that organ in mammals, but it has been questioned whether the homology was correct. Comparison has been made with man and the cat, and from the evidence at hand it would appear that the homology originally given was correct.

In Quain ('92), the essential relations of the *flocculus* of man are as here described, and Stroud's paper upon the cerebellum ('95) shows the same relations in its development. Dr. Stroud considers the mammalian *flocculus* to be a complex organ, a portion of which, the pugnus, in rodents, some carnivora, etc., lodged in a cavity of the petrous bone, is developed from a part a little removed from the caudal margin of the cerebellum. The question arises whether these facts can be brought into harmony, and the term *flocculus* be applied to the organ occupying a depression in the skull from whichever of the folia it arises, or whether there are really two different organs that have been called by the same name.

The simple *flocculus* of the sparrow is seen to be an offset from a primitive part of the cerebellum which lies next the edge to which the plexus is attached, with a special prolongation at the tip of the lateral recess. Fig. 24 shows with diagrammatic clearness the relations of this body to the mass of the cerebellum. The sheet of cinerea which in general is far from the cavity passes into the *flocculus* and with the last folium comes in contact with the caudal part of the cavity. In the embryo (Figs. 17-18) the condition is simpler, but still recognizable, though the caudal wall of the cerebellum is not so greatly developed. In the younger embryo the part could not be distinguished with certainty. In the *Amyda* a distinct *flocculus* was not found, but a ripa between the edge of the cerebellum and the plexus (Fig. 30) may be considered as the proton of the *flocculus*. In the alligator a still more marked rudiment of the part exists and the appearance in frontal section is quite similar to the embryo sparrow (Fig. 17).

## FIBER TRACTS AND COMMISSURES.

In the *Amyda* were traced over thirty fiber tracts, most of them being myelinic. These are, with their commissures, described under figure thirty-six (Fig. 36), where a numerical system of designation is adopted, in order to avoid too exact homologizing. In the turtle one is struck with the fact that few tracts are long. Tract 24, the posterior longitudinal fasciculus, is a marked feature of the *Amyda's* oblongata; it extends into the myel and is not as prominent as in the snapping turtle (Humphrey, '94). In the sparrow this tract is comparatively small. The optic tracts of the turtle are long, but as shown above, they are comparatively much shorter in the sparrow. In the base of the cerebrum of the turtle, and extending into the base of the oblongata, is an amyelinic system of fibers (2, 2, 2) which at first appears continuous. On closer scrutiny it seems to be interrupted by a cell nidus (k), which is so attenuated at its middle as almost to form two nidi. The remaining tracts are shorter, and in most cases it cannot be said that one, even with the intervention of a nidus, is a direct continuation of another. One tract fades out, another gradually increases, and from this fact one would suppose that the turtle's mental processes must be by slow and indirect methods.

In accordance with the greatly developed striatum in the sparrow, the union of the thalamus and striatum by tracts is correspondingly large. The tracts at the base of the striatum, extending cephalo-caudad through a great part of its length are also large. The mesal wall of the sparrow's cerebrum, as with some other birds (Bumm, '83, and Carss, '95) shows a great fan-like spreading of fibers, the handle of the fan passing into the thalamus mesad of the optic tract and disappearing in the caudal region of the infundibulum (Fig. 11). This seems to represent one portion of the complex system of fibers which in mammals is comprised under the name fornix. It is gathered from the entire hippocampal segment, both cephalad and caudad of the porta. In the *Amyda* only a few fibers could be in any way homologized with this tract.



The precommisure in both animals has a well developed strand passing caudad into the edge of the striatum. In the sparrow only this one portion could be distinguished. In the turtle it was seen to be composed of two parts, a myelinic and an amyelinic, while another part consisting of amyelinic fibers turns cephalad, but could be traced for only a short distance.

This brings us to the vexed question of the presence or absence of a callosum in these forms, in which, highly specialized as they are, a callosum might be expected to appear if it occurs in any forms below the mammals. In both cases a small commissure does exist dorsad of the precommisure in a position assigned by Osborn ('86-'87) to the callosum. Smith ('94) finds no evidence of a true callosum in the lowest mammals, and various investigators, both before and after Osborn are inclined to believe that in forms below mammals the commissure mentioned is a hippocampal or forni-commissure. Bellonci, '87-'88; Meyer, '95; Kingsbury, '95, are inclined to consider it is not a callosum. The name callosum is retained in this article for convenience merely. In the soft-shell as in the snapping turtle there are two amyelinic bundles, one passing dorso-caudad into the hippocampal segment as a kind of fornix, the other dorso-cephalad into the termatic eminence and thence into the hippocampal segment. Perhaps these, as Herrick, ('93), supposes, represent two distinct commissures, the forni-commissure and the callosum. As yet a complete homology of either of these parts with the so-called callosum of *Amphibia* does not seem to have been established. In the sparrow this commissure is so small as almost to escape observation; still, as in the turtle, it is distinct from the precommisure. In the latter quite a notch of endyma intervenes between the two (Fig. 29). In the younger embryo sparrow (Fig. 1) neither of these commissures had appeared in the thickened terma although the postcommisure is well developed.

The supracommissure of the *Anyda* is strongly developed; one portion lies in close proximity to the tube of the epiphysis, but no fibers could be traced to the epiphysis, as Herrick ('91) found to be the case in *Aspidonectes*. In correspondence with

the small habenæ the supracommissure of the sparrow is very slight. Even in the adult it was recognized with great difficulty and it is late in development, not a trace of it being found in the second embryo. This difference would be accounted for if the theory is correct which holds that the supracommissure is correlated in part with the epiphysis, especially in those forms in which the latter has an eye-like structure. The turtle is much more nearly related than the sparrow to forms in which a distinct eye-like structure is found.

The geminal (Sylvian) commissure is in the turtle well developed, in fact there are extensive commissural connections between two distinct sets of fibers, that lying ventrad of the great balloon cells being composed of large fibers, that lying next the endyma of fine fibers. In comparison with the large gemina only a small geminal commissure is present in the sparrow, the fibers taking a long course between divaricated gemina.

In the cerebellum of the turtle very close to the decussation of the fourth nerve in the valvula are two decussational tracts, the one from fibers of the cerebellum itself (tract 30, Fig. 36), the other more cephalic in position composed of fibers from the lateral surface of the oblongata cephalad of the fifth nerve (tract 29, Fig. 36). The latter is reinforced by fibers coming from a point caudad of the gemina and thus forms a great mass of fibers, which from its situation reminds one of the pons of mammals, but though fibers from it pass far toward the ventrimeson, none were found actually to cross. Arcuate fibers independent of this tract do cross the meson. Any conclusion with regard to a rudimentary pons in reptiles must depend upon a more thorough study of the origin of the pons in mammals. The commissure of the cerebellum in the sparrow (Figs. 11, 20, 24) receives fibers from the lateral parts of the cerebellum and even the flocculus, in this respect reminding one of the more caudal of the decussations in the turtle, and connects the great columnar peduncles which pass over into the acoustic eminence. There is no appreciable constriction separating the lateral part of the cerebellum from the acoustic eminence. This commissure of the cerebellum is the

second instance of a more complete union between the two sides in the sparrow than in the turtle.

#### CINEREA, NIDI.

In the adult *Amphibia* the cinerea is collected closely around the endyma, except in a few places where an incipient ecto-cinerea is found. It seems to be typical that cinerea should lie next the endyma, but it may be displaced from that position by growing fiber tracts, or fibers may so increase among the cells as to separate them. In both the turtle and the three stages of the sparrow, there are in many parts cells somewhat evenly distributed throughout the nervous tissue. In the youngest sparrow (Plate I) a concentration of cells is seen in most parts around the endyma, but already indications of layers and nidi of cells appear. In the adult the formation of layers and nidi has progressed much farther than in the turtle. In the latter there are around the rhinocœle three layers, more or less complete, separated from the endyma and from each other by fibers and surrounded by the glomerular layer (Fig. 37). In the sparrow only one group of cells could be distinguished, and that formed a central core for the coalesced olfactory lobes (Fig. 27).

In the turtle an incomplete layer of ectocinerea (Figs. 36, 31, 38-42) is especially noticeable in the pallial and hippocampal segments. In the sparrow a similar layer can be found only in the hippocampal region. The striatum in both animals is a mass of cells marked off by prominent bands of alba (Figs. 22-23).

In the habenæ the cells are arranged in hollow spheres, as shown by the rings of cells appearing in sections made in different planes (Fig. 25).

The geminum of the young embryo sparrow already shows indistinct layers (Figs. 2-5). Three such layers of greater condensation are seen, which become more pronounced in the next stage (Fig. 12). In this stage the number of distinct layers is the same as with the turtle (Fig. 31). In the adult sparrow the cinerea is divided into eight layers of cells, exclusive of the endyma, by fiber tracts.

The cinerea of the cerebellum of the turtle has an amphibian character in that the cells are near the endyma. They are interspersed by myelinic fibers and bordered by a layer of Purkinje cells. In addition to this, throughout the ectal alba, radiate rows of cells, and over the entire surface is a layer of small cells (Fig. 31). In the younger embryo sparrow (Fig. 6) a layer of cells preserving continuity with the endyma at the tela, is the only differentiation. It appears to be the same as the cellular layer which covers the surface in the next stage (Figs. 17-18), but in addition are found distinct nidi of cells. This ectal layer is confirmatory of the theory of Herrick ('91) that the cinerea of the cerebellum arises from the union of the solid parietes with a tela. In the adult the cinerea has assumed the segregated character found in mammalia, but retains its position next the endyma only at the meson, in the first and last folia (Fig. 36).

In structure as well as form the geminum and the cerebellum of the turtle have advanced about as far as the second embryo sparrow, while all the parts, including the cerebrum, have made about equal progress toward complete evolution, again showing the well-balanced condition indicated by the form. In the adult sparrow the cinerea of the cerebellum and gemina is highly developed, but in the cerebrum the arrangement of cells indicates, like the form of the parts, a high specialization aside from the more usual type of the mammalia.

As shown in the turtle (description of Fig. 36), there are besides these layers of cinerea at least twenty-six more or less distinct nidi of cells.

#### SULCI.

Perhaps one of the greatest contributions of recent years to the morphology of the brain is the discovery by His ('90) of the building up of the oblongata by a series of unions of the membranous portion with the edge of the solid parietes. Each so formed consolidation is a center for the proliferation of cells. This work is supplemented by that of Herrick ('91) on the cerebellum in which he found a similar process taking place. In 1893 in the article on *Diemyctylus* the writer recognized that in

other regions, as in the diencephal, definite furrows called *sulci* occur which have a morphological value in determining homologies, and which, at their deepest part, give origin to special cell masses. Humphrey ('94) in his study of the snapping turtle came to the conclusion that these sulci are of little morphological value and are determined mainly by fiber tracts or are incident to foldings of the wall. Since that time some progress has been made in studying these sulci. Those found in the turtle are enumerated under the description of Fig. 29. There appear to be three kinds of sulci; 1st, those just mentioned as discovered by His; 2d, those formed as the result of growing together of two symmetrical parts united by a membrane at the meson. The membrane apparently forms a U-bend and the original line of union on either side with the solid parietes forms the sulci, a lophius or ridge forming between them. What seems to be a striking example of this is seen in the roof of the cerebellum. Originally a membrane forms a roof-like connection between the two lateral halves (Fig. 6). In later embryos of both sparrow (Fig. 11, *r*) and the cat a small lophius is found extending a considerable distance along the meson. No trace of this was found in the adult sparrow, but in the turtle and the alligator a prominent feature of the cerebellum is a median lophius (Figs. 29-31, *l*) occupying a perfectly comparable position. The roof of the mesencephal in the turtle shows a similar sulcus and lophius (Fig. 29, *s*).

At the *crista* in these lower forms the solid parietes approach each other, but do not unite. There is a distinct U-bend with a sulcus on either side. The endymal cells forming the U are generally elongated and of a peculiar appearance. Figs. 8, 16, 26, 34, show that it occurs in the turtle and in different stages of growth in the sparrow. It always contains a blood vessel and sometimes more than one. Studnicka ('95) figures a similar appearance in Amphibia and shows its relations. He calls it the *terma*, but here is preferred the word *crista*, introduced by Wilder ('80), to indicate a small outgrowth upon the cephalic wall of the aula. This *crista* of the higher forms was identified by the writer

with an intrusion of endyma into the aula of *Diemyctylus* and *Amia* and has since been found in specimens of all the groups examined, except lamprey and shark, and with further study it is hoped to identify it in them. In the adult mammal it is obscured by the growth and crossing of hippocampal or fornix fibers cephalad of it, thus cutting it off from the pia and leaving it as a kind of record of development. It forms a valuable point of departure in determining the homologies of the region.

In the snapping turtle Humphrey ('94) figures a small mesal lophius or ridge in the floor of the metacæle but considers it without significance. A similar fold is found in the soft-shelled turtle (Figs. 29, 43,  $\varepsilon$ ), where it has only a short cephalo-caudal extent. It was sought in the sparrow, and in the embryo a mesal lophius was found, extending the length of the oblongata. Fig. 9 shows that from the sulci at either side extend layers of cells into the raphé, and that the slightly differentiated endyma at the side of those sulci corresponds with the limits of the raphé. The suggestion is made that these sulci give rise to the cells of the raphé, including the nidus  $\times$  (Fig. 36). A mesal lophius occurs in other parts of the floor of these brains, but special attention has not been given them.

Just ventrad of the postcommissure in both forms is the sulcus ( $\phi$ ). On closer examination this is found to be really a paired sulcus (Figs. 24 A, 32, 33), and hence can be homologized with the sulci composed of similar long, clear cells found widely separated ventrad of the postcommissure in the lamprey. All forms of vertebrates examined have such sulci. In the article on *Diemyctylus* they were homologized, following Rabl-Rückhard ('83) with the torus of fishes. There is now thought to be no such homology. The work of Loey ('93) upon the existence of a third pair of rudimentary eyes in sharks and *Amphibia*, is looked to with interest as throwing possible light on these structures, for they occur caudad of the entrance of the epiphysis, which he considers to result from the fusion of the second pair.

Sulci of a third class are those which occur upon the endymal surface of solid parieties, and give rise to nidi by complete union

of the walls of the sulci or by proliferation from the deeper layers ; the sulcus in the latter case continues as a feature of the endymal surface. In the brain of the young embryo sparrow are excellent examples of this class (Fig. 1, *h*, *n*, *p*). Sulcus (*h*) is a deep furrow, forming the caudal boundary of a lophius, which in frontal section (Fig. 3) is a noticeable feature just caudad of the porta. Caudad of the sulcus is the end of a fiber tract (*5*, in Fig. 1), which curves ventrad of it, then turns abruptly laterad into the striatum. In the second embryo the lophius and sulcus have almost disappeared (Figs. 11, 16, *h*), but the tract (*5*) retains its ventral curve, and a mass of cells shows the original extent of the sulcus. This mass of cells is recognizable in the adult. In the turtle the dorsal limb of the tract marked (*5*) in Fig. 36, takes a similar course to the above and ends at a great nidus (*d*), which seems to be homologous in position with the above mentioned mass of cells, although its relations to the endyma are obscured by the union of the endyma across the meson in the medicommissure. Sulcus (*e*, Fig. 29) just cephalad of the medicommissure may represent sulcus (*h*) of the sparrow. It is hoped from material now in hand to settle the matter of development of this and similar parts in the embryo soft-shelled turtle.

The sulci *n* and *p* are found in the embryo sparrow and in the turtle (Figs. 1, 4, 29, 32, 33). The first is comparable in position, according to Quain ('92), to a slit which "leads into the still hollow geniculate body." In the sparrow this sulcus disappears, but a cell nidus takes origin from it. The sulcus (*p*) does not disappear in either form, but in the early stage of the sparrow it is connected with a cell-mass which later separates from it. These two sulci give off nidi, which if compared with those of the turtle, seem to be homologous in position with nidi (*i*, *j* Fig. 36). One of these apparently represents the pregeniculum or "external geniculate body" of man.

On the mesal aspect of the caudal part of the geminum of the embryo sparrow is a furrow (Fig. 1, *G*). This forms a total fold of the wall and corresponds with an endymal ridge projecting

into the cavity (Fig. 4). This, soon uniting with the adjoining wall, divides the cavity into two parts, a mesal and a lateral (Fig. 5, *r. mc.*). In the next stage the mesal cavity is not present, but a nidus (Fig. 13, *N*) staining more deeply than the others, is seen to occupy (with reference to the cavities) a position which, when change of shape is taken into consideration, is found to be exactly comparable with the mesal part of the cavity above described. Nidus (q) (Fig. 36) of the turtle holds the same relative position, and from the fiber tracts of the region may be considered as the representative of a postgeminum, as suggested by Humphrey ('94).

Other sulci have masses of cells from their deeper parts which have not yet been identified. Some of these have morphological significance, however, independent of the nidi, as for instance those which enter the *porta*. In the turtle (Fig. 29) there are four sulci entering the *porta* which may materially aid in determining the real relations of that puzzling region. First, a small sulcus (*a*) is seen on the mesal wall of the projection of the *aula cephalad* of the *porta*. This enters the *porta* and turns cephalad upon the mesal wall of the *paracœle* and continues to the *precornu* (*pc'*). It indicates the line of junction between the hippocampal and termatic segments of the mesal wall of the cerebrum mentioned above. Second, a sulcus arising in the *preoptic recess* (*b*, Fig. 34) passes caudad of the *precommissure*, enters the *porta* (Fig. 35) and passes cephalad into the *precornu* (*pc'*, Fig. 29). Third, the sulcus (*d*) (Figs. 29, 35, 36) enters the *porta* and passes ventro-caudad to the *medicornu*, (*pc*). Fourth, the sulcus forming the dorsal boundary between the *habena* and *diatela* (Fig. 31, *g*) passes into the *porta* upon the mesal wall of the *paracœle* and forms the boundary between the *tenia* and the *paratela*.

The relations of the fourth sulcus show that the *paratela* is continuous with the *diatela* or roof of the *diacœle* and is thus in reality part of the roof of the *prosocœle*. This sulcus is morphologically at the lateral edge of the *rima*. At the opposite edge of the *rima* the sulcus there found unites with its opposite in the



region of the crista. In the sparrow this relation of the paratela is not quite as clear owing to the attenuation and distortion of adjacent parts.

Between the third and fourth sulci of the turtle a part of the thalamus lying cephalad of the medicommissure projects into the paracœle as shown at the right of figure 30. In this respect it agrees with the relations in the embryo cat as shown by Hochsteter ('94), a condition by no means to be confounded with the exploded notion that the rima allows a portion of the pial surface of the thalamus to enter the paracœle (Wilder, '84, '88). In the sparrow (Fig. 16) there is no medicommissure, but the essential relations are the same.

The mass included between the second and third sulci and their extensions represents the union of the striatum with the thalamus. According to His ('92) this mass should represent the cephalic continuation of the "Grundplatte" or ventral of the two segments into which he divides the lateral wall of the brain tube. In neither of the forms could be found that connection of either of the sulci bounding the mass with any more caudal sulcus which would indicate agreement with the explanation of His. The caudal sulcus in the embryo sparrow (Fig. 1, *d*) becomes shallow, but seems to be continuous with a sulcus extending to the optic recess.

In the sparrow (Fig. 1) occurs a marked peculiarity. The mass between the two sulci (*b* and *d*) rises flush with the general level of the cavity. It is an excessive growth of the caudatum forming a part of the lateral wall of the *aula*, and dividing the porta into two parts (Fig. 3). This becomes less apparent in the next embryo (Figs. 11, 16) and in the adult the growth of surrounding parts makes this condition noticeable only on account of its history. At first sight this seems to be quite different from the condition in the turtle; but the other relations of the sulci, including the mass, are identical.

Between the first and second sulci (Fig. 29, *a*, *b*) of the turtle lies the termatic outgrowth, extending from the thickened part of the terma, in which the commissures occur. It includes a part

of the preportal aula, and extends into the paracœle to the tip of the precornu. In the sparrow there is no preportal aula, but the part of the termatic outgrowth which bears the crista (Fig. 3, *c. e.*), is included wholly within the paracœle on account of the caudal extension of the mesal wall of the cerebrum, and the bounding sulcus can be traced to the precornu as in the turtle. A segment similar to this was found in *Diemyctylus* and recognized as termatic in its origin.

Dorsad of the first sulcus (Fig. 29, *a*) of the turtle is an aulic portion of the hippocampal segment. In the sparrow this, like the termatic segment, appears as if drawn entirely within the paracœle.

Thus upon the aulic surface of the cavities of the turtle, and potentially so in the sparrow, are represented all of the segments of the cerebrum, except the pallium.

The caudal boundary of the aula seems to coincide with the sulcus (*d*), or perhaps better the lophius caudad of it, extending from the porta to the optic recess. If this interpretation is correct it would appear to be more in accord with the researches of Studnicka than of His. Studnicka ('95) shows that in the early embryo of the lamprey and *Amphibia* there is a neuromeric, dorso-ventral, endymal furrow which bounds the "massive Anlage des Hemisphärenhirns," and that the division of the cerebrum itself into parts is by the formation of an independent intrusion of the cavity into the wall. This being the case, the pallium would not necessarily have a special aulic representative.

#### ADDENDUM.

The foregoing paper was read at the meeting of the society in August. While it was passing through the press the article by Burckhardt, "Der Bauplan des Wirbelthiergehirns" (Schwalbe's *Morphologische Arbeiten*, Vol. IV., 1895, pp. 131-149, 1 pl.), came into my hands. The colored diagrams show with great clearness his morphological views, and the text discusses with admirable force and directness the plan of the vertebrate brain, especially as shown by mesal structures. From a study of the

amphibian brain he derives a plan of the segments extending from the caudal end of the brain tube into the cerebrums. This plan is an extension and elaboration of the idea of His mentioned above (p. 217). The present paper reaches conclusions from entirely independent data; some of them agree with and some differ from those of Burckhardt, but more extended notice than could be given at present would be necessary justly to estimate the facts and bring them into that harmony which must be the ultimate result of complete knowledge.

## SUMMARY.

The points touched upon in this paper are :

1. The importance of comparing through all stages of development widely different forms of brains in order to gain from exaggerated form and specialized function more light upon the truths of morphology and evolution.

2. The overlapping and crowding of parts of the brain in these, which in comparison with others of the same groups, are highly specialized forms.

3. A degenerate condition of the olfactory lobes resulting in union due to crowding, not to a crossing of fibers from one lobe to the other. It is a feature incident to other specializations.

4. Although the parts connected with vision in the sparrow are highly developed the union of the gemina across the meson by a relatively small commissure would indicate an independence of action of the two sides in contrast with the condition in the turtle and other forms where the connection between the two sides is far more intimate.

5. The tip of the snout is a more important tactile organ in the turtle than in the sparrow, as indicated by the large branch of the fifth nerve distributed to it in the former.

6. The eighth nerve has reached a higher development in the sparrow than in the turtle as indicated by its intimate connection with its opposite across the meson and its apparent connection through the auditory eminence with the column-like peduncles of the cerebellum, which in their turn form a large commissural

connection in the cerebellum. These complicated and extensive structural developments and relations of these parts are probably associated with higher and more complex functions than the simpler conditions in the turtle.

7. The flocculus of the sparrow is probably homologous with the organ of the same name in man, and has a proton in the turtle and alligator. The pit in the skull for the reception of the flocculus is formed before the flocculus has grown sufficiently to enter it.

8. Twenty-six *nidi* and more than thirty fiber tracts with their commissural connections were found in the turtle and many apparent homologues were recognized in the sparrow. Especially in the turtle there is not the continuity of nerve tracts which one is led to believe occurs in mammals, but there is rather a more or less independent, overlapping series of tracts.

9. The pons is not present.

10. In the sparrow a large fiber tract from the mesal wall of the cerebrum strongly suggests the fornicolumn of mammals, but it has more extensive relations.

11. The conclusion is adopted that the so-called callosum of birds and reptiles is the rudiment of a fornicommissure with a few fibers which may be truly callosal.

12. A metapore was not demonstrated in either the sparrow or soft-shell turtle, although the tela is very much attenuated in the position usually assigned to the metapore.

13. The metaplexus is apparently formed by crowding a V-shaped membrane between two nearly parallel edges of the cerebellum and the oblongata.

14. The roof of the epicele is at first a membrane. The union of the lateral halves of the cerebellum across the meson is secondary, the connecting membrane being replaced by a mesal lophius.

15. The widely divaricated condition of the gemina in birds is not due to crowding by the cerebrum and cerebellum, but to their intrinsic growth, nearly completed before any crowding could occur.

16. There is suggested the possible identity of the double sul-

cus ventrad of the postcommissure with the pair of lateral outgrowths occurring caudad of the epiphysis, discovered by Locy.

17. The diaplexus of the turtle consists, in large part, of foldings of the membrane at either side of the meson. In this respect it has a closer relationship with the mammalian type than the mesal plexus of either the bird or the amphibian.

18. In both turtle and sparrow the paratela, occupying the rima, or interval between the fimbria and the tenial edge of the striatum, is morphologically a part of the roof of the prosocœle.

19. Various pockets of endynia were found upon the meson, which have great significance for morphology, but are physiologically of slight importance. Among these pockets is the paraphysis, found in the adult *Anyda* and in the embryo sparrow.

20. In *Amphibia*, turtle and sparrow, a transection of the hemi-cerebrum shows essentially a delta form. Caudad of the rima the three limbs are: (1) The ventral or striatal; (2) the lateral or pallial; (3) the mesal. The first two form segments extending from the caudal tip to the olfactory lobes. The rima divides the mesal segment into two parts, the dorsal or hippocampal, and the ventral or tenial. At the porta the tenial unites with the thalamus. Cephalad of the porta the hippocampal unites with an outgrowth of the terma, the termatic segment; so that in the cephalic part of the brain the same complete delta form is re-established.

21. Sulci which enter the porta indicate that the hippocampal, termatic, striatal and tenial segments of the cerebrum have a representative in the mesal wall of the aula (cephalic part the third ventricle).

22. In both the sparrow and the turtle the striatal limb of the delta has a secondary thickening, which is comparable with the caudatum of mammals.

23. The porta of the embryo sparrow is bifurcated by the intrusion of the caudatum into the aula. In the adult this intrusion is crowded into insignificance by surrounding parts. The two sulci of the aula which enter these parts of the porta can be

traced upon the wall of the parocœle, one extending cephalad and the other caudad. On the aulic surface these sulci pass ventrad with no appearance of turning caudad to form the aulix or sulcus of Monro, as the theory of His would seem to demand. Comparable sulci entering the porta were found in the turtle, although the caudatum does not intrude into the aula.

24. The significance of other sulci was considered. (1) Those which indicate the boundary of a primal mesal membrane as in the cerebellum and at the crista; (2) those occurring at the edge of solid parieties as in the formation of parts of the oblongata, as shown by His, or of the cortex of the cerebellum, as shown by Herrick; (3) those occurring in more solid parts, and whose walls finally coalesce to form a cell nidus.

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## EXPLANATION OF PLATES.

Roman numerals, I. to XII, indicate the cranial nerve roots. Arabic numbers indicate fiber tracts. Italic letters represent sulci. Roman letters indicate nidi. For a complete enumeration of the nidi, tracts and sulci see explanation of Figs. 29, 36.

## ABBREVIATIONS.

<i>ap.</i> .=auli-plexus	<i>gl.</i> .=glomeruli	<i>P.</i> .=Purkinje cells
<i>au.</i> .=aula	<i>gm.</i> .=geminum	<i>par.</i> .=paraphysis
<i>b.v.</i> .=blood vessel	<i>hb.</i> .=habena	<i>pc.</i> .=paracœle
<i>cal.</i> .=rudimentary cal- losum or fornicom- missure	<i>hy.</i> .=hypophysis	<i>pcm.</i> .=precommissure
<i>cbl.</i> .=cerebellum	<i>inf.</i> .=infundibulum	<i>pia.</i> .=pia
<i>c.e.</i> .=termatic eminence	<i>inf. cm.</i> .=commissures of the infundibulum.	<i>pl.</i> .=pallium
<i>ch.</i> .=chiasma	<i>mb.</i> .=membranes	<i>poem.</i> .=postcommissure
<i>cr.</i> .=crista	<i>mc.</i> .=mesocœle	<i>pp.</i> .=paraplexus
<i>Dien.</i> .=Diencephal	<i>mcm.</i> .=medicommissure	<i>Prosen.</i> .=Prosencephal
<i>dp.</i> .=diaplexus	<i>Mesen.</i> .=Mesencephal	<i>pt.</i> .=porta
<i>dt.</i> .=diatela	<i>Meten.</i> .=Metencephal	<i>R.</i> .=Recess from aula ventrad of crista
<i>ec.</i> .=epicœle	<i>m.p.</i> .=mesencephalic pit	<i>re.</i> .=rhinocœle
<i>el.</i> .=endolymphatic sac	<i>mst.</i> .=mesotela	<i>Rhinen.</i> .=Rhinancephal
<i>end.</i> .=endyma	<i>mt.</i> .=metatela	<i>rm.</i> .=rima
<i>Epen.</i> .=Ependecephal	<i>mtc.</i> .=metacœle	<i>rnc.</i> .=recess of mesocœle
<i>epi.</i> .=epiphysis	<i>mtp.</i> .=metaplexus	<i>S.</i> .=Endymal pocket cau- dad of postcommissure
<i>et.</i> .=epitela	<i>my.</i> .=myel	<i>scm.</i> .=supracommissure
<i>F.</i> .=Fissure between ol- factory lobe and cere- brum	<i>myc.</i> .=myelocœle	<i>st.</i> .=striatum
<i>fm.</i> .=fimbria	<i>N.</i> .=Nidus in the gemi- num	<i>ter.</i> .=terma
<i>fl.</i> .=flocculus	<i>nc.</i> .=notochord	<i>th.</i> .=thalamus
<i>G.</i> .=Fissure on the gemi- num	<i>obl.</i> .=oblongata	<i>v.cm.</i> .=ventral commis- sure
	<i>op.r.</i> .=optic recess	

The mesal views are reconstructed from sagittal, frontal and transections. Faint outlines indicate the hidden parts of the cerebrum, the geminum and the paraplexus. The outlines of lateral cavities are indicated by interrupted lines. The position of the eye and of nerve roots is indicated by fine interrupted lines.

Numbers and reference lines indicate upon the mesal views the level at which the sections figured were made.

## PLATE I.

Fig. 1. Mesal view of the brain of an embryo sparrow, the general state of development of which corresponds quite closely with a chick of 10 days' incubation as figured by Duval ('89).  $\times 17$ .

Special attention is called to the following: The recess (R.) cephalad of the thickened terma in which later the cerebral commissures develop; the membranous roof of the diacœle (*dt*); the large, open epiphysis; the absence of a supracommissure; the post and geminal commissures; the large opening of the mesocœle into its lateral recess; the fissure (G) upon the mesal surface of the geminum; the membranous roof of the mesocœle (*mst.*), and the epicœle (*et.*); the small metaplexus (*mtp.*); the thin walled sac extending over the myel (*mt.*); the deep sulci on the endymal surface; the appearance of a portion of the striatum in the aula, dividing the porta into two parts; the independence of the olfactory lobes.

Fig. 2-7. Frontal sections of the series from which Fig. 1 was constructed.  $\times 9$ . The undifferentiated membrane (*mb.*) from which pia and arachnoid develop, is shown at the left.

Fig. 2. Shows the paraphysis in the midst of undifferentiated membrane; the rudiment of a paratela (*rm.*) and paraplexus; the union of the left recess of the mesocœle with its dorso-mesal extension.

Fig. 3. Shows the intrusion of the striatum into the aula and the division of the porta into two parts.

Fig. 4. Shows recess (R) cephalad of the terma; the aulic and paracœlic parts of the sulci (*b* and *d*); the deepest parts of sulci (*h* and *n*); the fibers to the postcommissure.

Fig. 5. Shows sulci (*j. k.*); the two parts of the recess of the mesocœle produced by the total fold (G).

Fig. 6. Shows lateral halves of the cerebellum connected by a membrane (*et.*); ectal cells (*jl*) continuous with the membrane.

Fig. 7. Shows lateral extent of metatela.

Fig. 8-10. Details from the same series.  $\times 45$ .

Fig. 8. Shows entrance of sulcus (*b*) into the ventral angle of the porta; the crista between the wide termatic segments (*ec*).

Fig. 9. Shows mesal lophius between sulci (*z*) and cells extending from them into the raphé.

Fig. 10. Shows sulci (*o* and *p*) which pass ventrad of the postcommissure.







## PLATE II.

Fig. 11. Mesal view of the brain of a half-grown embryo sparrow.  $\times 16.5$ . Compared with figure 1, the mesal extent is seen to be not much greater; development has consisted in lateral growth, thickening of parts and change in direction of the brain tube.

Attention is called to the fibers on the mesal aspect of the cerebrum which unite and pass into the thalamus; the small protrusion of the striatum into the aula; the decreased sulci of the cephalic region; the small entrance from the mesocœle to its lateral recess; the close approach of the well developed geminum to the chiasma; the union of the olfactory lobes.

Fig. 12-13. Frontal sections from the series from which Fig. 11 was constructed.  $\times 7$ .

Fig. 12. Shows short course of optic tracts (11) from chiasma to gemina.

Fig. 13. Shows nidus (*N*) occupying the position of the mesal part of the lateral recess (Fig. 5). Nidi near the raphé are of the third and fourth nerves.

Fig. 14-18. Details from the same series.  $\times 12$ .

Fig. 14. Shows relations of auli and diaplexuses dorsad of the porta.

Fig. 15. Shows the portas and plexuses.

Fig. 16. Shows at the left, the bifurcated porta; at the right the union of the striatum with adjacent parts ventrad of the porta; the aulic and paracœlic parts of the sulci (*b* and *d*); the united hippocampal and termatic segments (*e. e.*), containing fornix fibers; a tract crossing the striatum from the thalamus; a tract from the thalamus to the cerebrum; the mesal diaplexus.

Fig. 17. Shows, at the left, the flocculus and its relations to the depression in the skull filled with connective tissue (*mb*); at the right the entrance of the epiplexus which is (Fig. 18) continuous with the metaplexus.





## PLATE III.

Fig. 19. Sketch of the dorsal view of the brain of an adult English sparrow.  $\times 1$ . It shows the globular form of the brain and the overlapping of the segments, the mesencephal and the metencephal not being visible.

Fig. 20. Mesal view of the same.  $\times 8.5$ . Compared with similar views of the embryo (Fig. 11), it shows that the eye and the brain have become more separated; and that, considering the relative magnification (at the same scale as Fig. 11, Fig. 20 would be twice as large), the area of the chiasma has greatly enlarged; in length the cerebrum has increased threefold, the cerebellum five and the oblongata two, the union of the olfactory lobes threefold and the geminum one-third. Attention is called to the comparatively smooth endymal surface; the well marked ectal cinerea of the cerebellum and its 13 folia; the epicœle partially occluded at the meson; the caudal wall of the infundibulum nearly fused with the oblongata; the greatly elongated, partially closed tube of the epiphysis; the small supra-commissure; the long stretch of membrane between the entrance of the epiphysis and the postcommissure; the minute opening of the mesocœle into its lateral recess.

Fig. 21-23. Transections of the same.  $\times 3.3$ .

Fig. 21. Shows the cephalic, solid portion of the cerebrum and the united olfactory lobes.

Fig. 22. Shows the small portas and paracœles; the layers of alba and cinerea in the striatum; the ventral position of the gemina.

Fig. 23. Shows the opening of the mesocœle into its lateral recesses and its wide membranous roof.

Fig. 24. Frontal section of the same. The level at which this section was made is indicated by the (24) at the right of Fig. 20. This figure shows the cerebellum, its commissure, cavity and a nidus at either side; a continuous sheet of ecto-cinerea extending into the flocculus and caudad of the epicœle forming an ento-cinerea.

Fig. 24 A. An enlarged view of the double sulcus (*o*) on the cephalic aspect of the postcommissure.

Fig. 25-27. Details of the same series.  $\times 22$ .

Fig. 25. Shows habenas with their peculiar annular arrangement of cells; the diaplexus and paraplexuses; ventrad of the diacœle, the membrane connecting the tube of the epiphysis and the postcommissure.

Fig. 26. Shows the crista; the wide termatic eminence (*c. e.*); the entrance of the sulcus (*d*) into the paracœle at the cephalic angle of the porta.

Fig. 27. Shows the fusion of the cinerea and of the glomerular layer in the olfactory lobes.







## PLATE IV.

Fig. 28. Sketch of the dorsal view of the brain of an adult *Amyda mutica*.  $\times 1$ . It shows a portion of all the segments.

Fig. 29. Mesal view of the brain of a young *Amyda mutica* (13 cm, across the carapace).  $\times 9$ . Especial attention is called to the symmetrical development of the segments, the uniformity of commissural relations in the different segments; the union of the olfactory lobes; the paratela, faintly outlined, extending from the porta to the medicornu (*pc.*); the projection into the cavity of the callosum and precommissure; the close approach of the paraphysis and epiphysis dorsad of the diaplexus.

*Sulci.*—(*a*) From preportal aula into the precornu; (*b*) from preoptic recess to precornu; (*c*) laterad of crista; (*d*) from aula to medicornu; (*e*) cephalad of medicommissure; (*f*) defines medicommissure; (*g*) dorsad of habena joined by (*h*) ventrad of habena, the sulcus formed by the union of these passes through the porta to form the boundary between the paratela and tenia; (*i*) in the roof of the diacœle at either side of the paraphysis and epiphysis; (*j. k.*) in the optic recess; (*l*) the deep infundibular sulcus with its branches to the different recesses of the infundibulum; (*m*) sulcus between the ventral and infundibular commissures; (*n*) cephalad of the postcommissure; (*o. p.*) following the outline of the postcommissure; (*q*) extending into the cephalic end of the slit-like passage from the mesocœle to its lateral recess; (*r. s.*) entering caudal end of the same; (*p*) defining the mesal lophius of the cerebellum; (*u*) bounding the entrance of the metaplexus (compare Fig. 36); (*v. w.*) ventrad of (*u*); (*x*) laterad of the posterior longitudinal fasciculus; (*y*) in the metatela; (*z*) defining the mesal lophius of the oblongata.

Fig. 30-31. Frontal sections of the same.  $\times 4.2$ . The union of the olfactory lobes is shown, the cavities and plexuses of the cerebrum; the narrow cerebellum with its mesal lophius (*t*), entocinerea and Purkinje cells. For tracts and nidi, see Fig. 36.

Fig. 31 shows meso-dorsal part of mesocœle and its lateral recesses.

Fig. 32-35. Details from same series.  $\times 19$ .

Fig. 32-33. Show relations of sulci in the region of the postcommissure. The double sulcus (*o*) extends upon a mesal fold of tissue caudad of the postcommissure.

Fig. 34. Shows the crista and the entrance of the sulci from the aula to the paracœle at the ventral angle of the porta.

Fig. 35. Shows the preoptic recess cephalad of the precommissure and the origin in it of sulcus (*b*); the relation of other sulci to the medicommissure.